Pacific Science (1983), vol. 37, no. 4

The Possum and Rata-Kamahi Dieback in New Zealand: A Review[1]

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ABSTRACT: Browsing by the introduced Australian brush-tailed possum (*Trichosurus vulpecula*) has been generally accepted in New Zealand during the past 30 yr as the principal cause of damage to hardwood forests dominated by rata (*Metrosideros spp.*) and kamahi (*Weinmannia racemosa*). Recently, this view has been challenged, and assertions have been made that the forests in a North Island tract were in poor order before possums invaded, that their natural collapse was only a matter of time, and that there is ample evidence relating the more dramatic changes in South Island forests to geological and meteorological events. In this paper, the evidence for repeated coincidence of increase of possum numbers and spectacular modification of the forests is reexamined. Such coincidences, the continued good health of montane hardwood forests where possums have not attained high numbers, and some experimental data, lead to the conclusion that the possum is responsible for dieback in rata–kamahi forests. Control of possums is therefore vital if the forests are to be maintained.

THE EFFECTS OF BROWSING by possums have been debated in New Zealand for the past 70 yr, with opposing views that the animal is a valuable addition to the fur-bearing fauna, or that it damages indigenous forest, orchards, plantations, and conservation plantings. These topics have been extensively reviewed by Holloway (1959), Howard (1965), Kean and Pracy (1949), McKelvey (1959), Poole (1959), Pracy (1974), Veblen and Stewart (1982*a*), and Wodzicki (1950).

Over the past 30 yr, the possum has become generally regarded as "the number one problem animal. They present a major and immediate threat to the safety of the mixed hardwood (rata–kamahi) forests, as anyone familiar with the situation in Westland or the Southern Ruahines will be well aware" (Holloway 1973:127). Accordingly, poisoning programs against possums have been undertaken, with priority in mixed hardwood forests where the potential economic consequences of erosion damage to downstream farms and other economically measurable values are greatest. Such off-site values are usually emphasized because of the difficulty of placing an economic value on the aesthetic, hydrological, or biological importance of montane forests.

Two recent papers question whether the erosion consequences of forest damage or the degree of modification due to browsing of rata (*Metrosideros robusta*)–kamahi (*Weinmannia racemosa*) are as significant as supposed. Mosley (1978:21), writing on erosion in the southeastern Ruahine Range, concluded that "deterioration of the forest cover, *which appears to be fundamentally natural* but perhaps exacerbated by introduced animals, may have been a factor; the introduced animals have probably been responsible primarily for prolonging the period of above-average erosion by *retarding recovery* of the forest cover" (my italics). In similar vein, Veblen and Stewart (1982*a*:392) wrote: "although browsing by possums is certain to have caused some shifts in the relative abundance of some tree species, demonstration of the magnitude of such shifts has proved intractable. In Central Westland rata (*M. umbellata*)–kamahi forests, it is not clear the degree to which the excessive tree

[1] N.Z.F.S. No. 1687/ODC 182.2:451.2. Manuscript accepted 5 October 1983.

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mortality should be attributed to possum browsing as opposed to natural stand dynamics. Given that introduced wild animals have been present for more than a century and have had a pervasive influence on the vegetation of the entire country, it is a daunting task to separate natural from animal-induced change. However, *there is ample evidence relating the more dramatic changes in the forests of the South Island to geologic and meteorological events* or to direct human activities such as burning" (my italics).

Has possum control in the rata–kamahi forests therefore been a futile effort to maintain forests that were changing as a result of innate dynamic processes?

In this review I contend that browsing by the introduced possum is the essential causal element of extensive dieback of rata–kamahi forests (and *Fuchsia*-dominated seral scrub). But it is an *additional* element. I do not contend that the forests would not change over time in the absence of possums. Nor does my contention conflict with emerging evidence of the importance of autecological characteristics of vulnerable species (of which population dynamics are an aspect), diseases, insect attacks, storms, and other stresses. I accept the widely accepted hypothesis that the invasion and increase of possums is influenced by removal of understorys by the introduced ungulates (Holloway 1959, Kean and Pracy 1953, McKelvey 1973). I do not assert that all the loss of foliage from damaged trees is attributable to the feeding of possums. The direct effect may range from complete defoliation to just sufficient foliage being removed to alter the vitality of a tree, allowing the entry of pathogens, or to reduce its resistance to insect attack or disease. The removal of foliage may be more significant in the alteration of the microclimate within stands, their wind-resistance, or any other imaginable succession of events. Whatever the balance of mechanisms in a particular place, I still come to the conclusion that without the possum, the mixed hardwood forests would not have died back in the spectacular and abrupt manner we have witnessed over the past 30 yr. The evidence for this argument is repeated coincidence of two events—increase of possums and the onset of dieback—and of its corollary—that where possums have not occurred in high numbers, the forests are healthy.

By far the most dramatic examples of dieback are those in the southern Ruahine Range of North Island, and central Westland of South Island. Since Stewart and Veblen, Payton, and Allen and Rose describe central Westland forests in this issue, I shall emphasize the Ruahine Range and the nearby Manawatu hills in North Island.

THE RUAHINE EXAMPLE

The general sequence in the Ruahines has been described by Elder (1958, unpublished N. Z. Forest Service Report; 1965) and reviewed by Cunningham (1979). Possums were liberated in the district at several sites from 1893 to 1936 (Pracy 1974), and populations spread into the mid-altitude forests in the late 1940s and 1950s (I. L. James and P. E. Beaumont 1973, unpublished New Zealand Forest Service Protection Forestry Report No. 80).

Defoliation of kamahi had become conspicuous by 1955. By the mid-1960s, a large proportion of the seral scrublands and rata (*Metrosideros robusta*)–kamahi forests had collapsed (Figures 1, 2) and been replaced by vegetation dominated by grasses and ferns, with occasional shrubs and nonpalatable species.

In his assessment of this collapse and its erosion consequences, Mosley (1978:30–32) stressed the possible importance of other factors besides the invasion of possums and the two ungulates *Capra hircus* and *Cervus elaphus*. He repeated a comment by Elder (1958, unpublished N. Z. Forest Service Report), who had noted the early death of kamahi on exposed ridges and steep faces and had suggested that the effects of drought ought not to be dismissed as negligible; that much of the dead and dying forest was old and even-aged; and that gales, cloudiness, and insects should be considered. In summarizing, Mosley suggested (1978:32) "the evidence indicates that the forest cover was

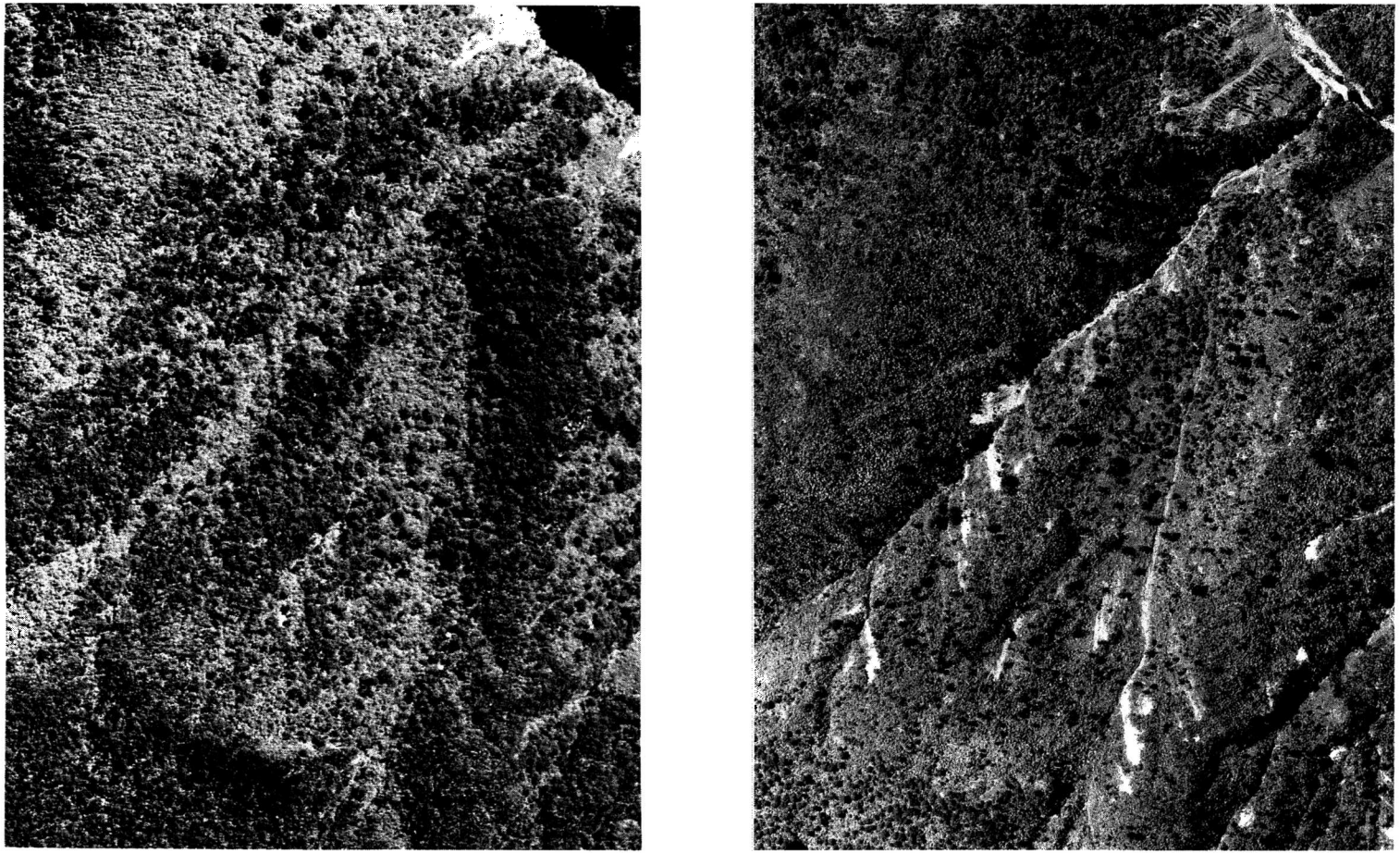

FIGURE 1. Typical example of collapse of *Weinmannia* forest and *Fuchsia* scrubland between 1946 (left) and 1978 (right) in the Pohangina catchment, southern Ruahine Range. Only isolated trees (mainly *Podocarpus ferrugineus*) remain of the tall forest in 1946. That and the extensive *Fuchsia* (light color) have been replaced by *Pseudowintera* scrub (pin cushion texture), *Melicytus* in scattered clumps and isolated shrubs, open grass/forb vegetation, bare soil, and scree. Note the exposure of the stream channels and increased extent of eroded surfaces. North is at top of photographs; area is approx. 44 ha. (Photographs 560–60, 1946; 0–24, 1978; courtesy Department of Lands and Survey.)

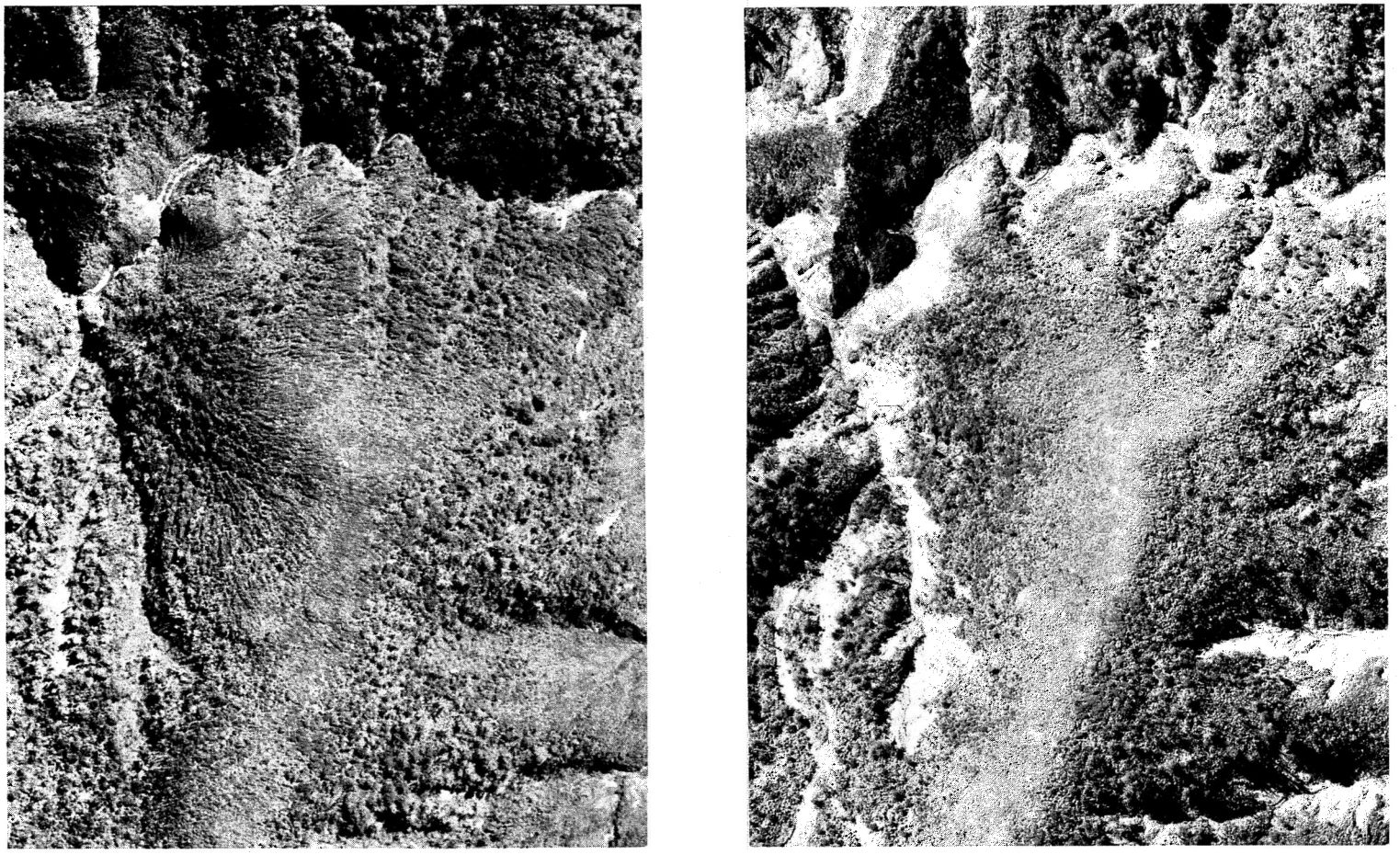

FIGURE 2. Collapse of both wind-furrowed and sheltered *Weinmannia* forest in Cattle Creek, Pohangina catchment, between 1946 (left) and 1978 (right). Most replacement is in *Cyathea–Histiopteris* fern scrubland, with pronounced increase in the extent of eroded surfaces. North is at top of photographs; area is approx. 44 ha. (Photographs 560–64, 1946; Q-29, 1978; courtesy Department of Lands and Survey.)

unhealthy well before animals became a significant influence, and that severe weather conditions in the 1930s and 1940s may have triggered a dramatic collapse whose eventual occurrence was only a matter of time."

This conclusion has far-reaching implications for management of the forests. Would the forests have collapsed without the effects of browsing by possums and other introduced animals? Would the defoliation have been reversed if possums and ungulates had been effectively controlled? In answer, it is important to ascertain the condition of the forests up to the 1940s, because if they were in poor order before possums became established, possums cannot be implicated as a major cause of collapse.

Unfortunately, the greatest changes occurred before the vegetation of the Ruahines was studied in detail. Much of the available literature therefore depends upon recollections, and most of it lacks objective evidence. However, even the most cursory examination of aerial photographic surveys of the range made in 1946, 1963, 1974, and 1978, reveals spectacular changes between 1946 and 1978. For this review, I compared the 1946 and 1978 photographs using 100-dot grid positions at 13 systematic matched sample points covering the Pohangina catchment (the largest southern Ruahine catchment). High forest covered 74% of the catchment in 1946, and only 6% in 1978. Tall scrub (principally *Fuchsia excorticata/Aristotelia serrata* in 1946) declined from 20% to 13% (principally *Pseudowintera colorata/Melicytus ramiflorus*) in 1978. By 1978, short scrub species, grasses, ferns, and other herbaceous species covered 69% of the surface. Scree and bare ground increased from 0.4% to 6% (Table 1). Examination of photographs of other catchments suggested that these changes in the Pohangina are representative of the kamahi forests throughout the range. I could not see any general evidence for Mosley's assertion that the vegetation (as distinct from the slip sites) was unhealthy in 1946—before the buildup of possum numbers.

The 1946 aerial photographs show erosion scars related to a recent storm, presumably the 1936 episode referred to by Mosley (1978) and James (1973). Apart from some photographs taken in the lower reaches of southeastern catchments (Mosley 1977, 1978), where there had been intermittent fires, cattle had been present for decades, and the easily accessible timber had been removed long before 1936, no other information is available on the effects of the 1936 storm in the Ruahines. Zotov et al. (1939:270) described it for the Tararua Range further south as a "once in a lifetime" cyclone that leveled whole hillsides of forest in 2 hr. Even if one assumes that this storm significantly affected the Ruahines, the 1946 photographs show (as summarized in Table 1 and illustrated in Figure 1) smooth-canopied *Olearia colensoi* subalpine scrub at the higher levels, gully scrub associations dominated by *Fuchsia* and *Aristotelia*, tall close-canopied kamahi, wind-furrowed kamahi on the exposed faces and ridges, and multiple-tiered podocarp/rata/kamahi forests on more sheltered sites. Thus, the photographs portray a forest ecosystem in the late 1940s that was sufficiently resilient to absorb the shock of any episodes such as the 1936 storm, which had happened within the life-spans of the large podocarps, rata, kamahi, and other forest dominants.

This interpretation is consistent with

TABLE 1

AERIAL PHOTOGRAPH SURFACES AT 1300 POINTS IN THE POHANGINA CATCHMENT, 1946 AND 1978

COVER TYPE	COVER (%) 1946	1978
Multitiered tall forest	39.5	5.2
Wind-canopy *Weinmannia*	3.5	0
Smooth-canopy *Weinmannia*	30.8	1.2
Tall scrubland	20.0	13.4
Low scrub, dead trees over scrub	0	43.1
Cortaderia–Chionochloa	0	11.4
Grass/fern forb cover	0.2	14.5
Bare ground and scree	0.4	5.9
Riparian scrub/grass	1.0	1.2
Stream channels	1.9	2.5
Shadow	2.5	1.6

NOTE: Tall forests dominated by *Weinmannia* made up 74% of the 1946 cover and 6.4% in 1978. Low scrub, dead trees over scrub, and *Cortaderia/Chionochloa* tussock increased from 0% to 53.5%.

Elder's (1958:13, unpublished N. Z. Forest Service Report; 1965) conclusion that there was "practically no evidence of damage due to deer or possums" up to 1940. However, by 1948, 19 tree and shrub species were being defoliated by possums (Elder 1958:13–14, from L. T. Pracy, unpublished Internal Affairs Department Report): "Canopy defoliation was becoming conspicuous from the plains ... and by 1955 widespread death of canopy had attracted general notice and was reported from several quarters almost simultaneously." Droughts, disease, insect epidemics, earthquakes, and fires were also considered as possible causes, but in Elder's view, the absence of evidence for any major natural cause coupled with the abundance of possum sign and their diagnostic browsing pattern implicated the possum. Elder again reviewed the situation 7 yr later: "Animal damage has been most spectacular in the almost complete defoliation of the canopy by possums over large areas of *Weinmannia*-dominant forest in the southern Ruahines" (Elder 1965:47). James (1973:96) subsequently noted: "the former rata–kamahi forest canopy was killed by possums during the 1950s, and has generally collapsed leaving only scattered trees of species not preferred by possums." Esler (1978:49–51), working in the rata–kamahi forests of the Manawatu hills southwest of the Ruahines recorded, "the vegetation is no longer northern rata–kamahi forest but a mosaic of shrubland and grassland ... the kamahi took on a greyish appearance as it was defoliated by possums. The defoliation was closely examined and there was not the slightest doubt about its cause."

Thus, the available evidence indicates that up to the late 1940s the forest vegetation of the Ruahine Range and nearby hills was in good order. Beyond that time, the evidence establishes the coincidence of the eruption of possums and collapse of the forests from the late 1940s continuing into the 1960s.

Such changes in the Ruahine rata–kamahi forests cannot be described as "decline," as used in connection with Hawaiian *Metrosideros* forests (Papp et al. 1979). Neither are they compatible with the assumption that the possum "has caused some shifts in the relative abundance of some tree species" (Veblen and Stewart 1982*a*:392). These forests, previously in apparently good order, collapsed over several thousands of hectares soon after possums, deer, and goats reached high numbers.

OTHER REGIONS

Elsewhere, the pattern is essentially the same. In the Urewera forests of northeastern North Island, a series of surveys by Wallis and James (1972) and G. T. Jane (1978, 1979, unpublished N. Z. Forest Service Reports) led to the general conclusion that the possum has browsed and killed out many species of plants, and that the progressive depletion of *Fuchsia*, *Aristotelia*, with other characteristic species, determined the stage of possum colonization in any area. Jane noted that *Metrosideros robusta* and kamahi were eliminated from the canopy about the time possums reached peak density. Dying forests occurred in concentric zones surrounding liberation points (Wallis and James 1972) and affected all age classes of forest (e.g., see Howard 1965:59).

Fitzgerald (1976) reviewed the evidence for the Orongorongo Valley near Wellington, where the forest had been under observation since the 1940s. Possum numbers reached peak density about 1940. By 1976, *Fuchsia excorticata* and *Alectryon excelsum*, formerly common and preferred foods for possums (Mason 1958), were rare and constantly browsed. Dead or substantially defoliated *Weinmannia* were common; the survival of *Beilschmiedia tawa* and *Pseudopanax arboreus* appeared to be threatened; only a few *Myrsine salicina* survived. In the same area, Meads (1976) recorded the defoliation by browsing and the subsequent death of 11 of 50 *Metrosideros robusta* over the years 1969–1974, and the recovery to full canopy of 5 trees that were protected from possums by metal sheaths.

The evidence for Westland southern rata (*Metrosideros umbellata*)—kamahi forest is similar to that for the North Island. Collapse

of forests in substantial areas of the north bank of the Kokatahi River has been the subject of many reports (Holloway 1959, I. L. James, G. T. Jane, and C. Barr 1973, unpublished N. Z. Forest Service Protection Forestry Report No. 116; Travers 1964), spectacular photographs, and continuing research. The effects of possums in other areas have been described by Bamford (1972), L. W. Best and P. S. Crozier (1970, unpublished N. Z. Forest Service Protection Forestry Report N. 74), Coleman, Gillman, and Green (1980), and Pekelharing (1979). Of these reports, Pekelharing's (1979) synthesis of the sequence of events on the north bank of the Taramakau River is typical. Possums spread into the area sometime after 1950, and a wave of canopy defoliation progressed upriver as the animals attained high densities. The same sequence has occurred in montane forests throughout Westland. But where possums are absent, or as yet only in low numbers (e.g., Whitcombe Valley, Copland Valley), the forests appear healthy.

STAND DYNAMICS OR POSSUM DAMAGE?

This account could be expanded by other reports of the sequence of possum invasion and collapse or modification of the rata–kamahi (and seral *Fuchsia–Aristotelia* scrub) associations throughout New Zealand, but this would add little to an understanding of causality. The examples already given implicate possum browsing as the principal cause of rata–kamahi dieback by the consistent lack of notable dieback where possums are absent or present only in low numbers, and the experimental reversal of defoliation of trees by protecting them from possums.

Doubts about this conclusion have been expressed many times. Most recently, Veblen and Stewart's (1982*a*) thesis, while conceding that possums may have had a pervasive effect on the forests and caused some shifts in the abundance of some tree species, clearly argues that the more dramatic events in South Island forests are related to geological and meteorological events—that is, earthquakes, storms, droughts, and long-term climatic changes. They mention historical evidence suggesting that the forests have always been relatively unstable: the occurrence of dead trees in photographs of Westland forests in 1907, long before possums occupied the region in any numbers; and the speculation of early explorer Charles Douglas about the possible earthquakes and storm origin of the conspicuous even-aged stands of rata in the Westland montane forests. Similarly, C. H. Tyndale-Biscoe (in C. G. R. Chavasse 1955, unpublished N.Z. Forest Service Report) mentioned evidence of changes in rata forests of the sub-Antarctic Auckland Islands between the 1880s and 1954. Elder (1958, unpublished) drew attention to a 1907 report by L. Cockayne (which I have not been able to find) that mentioned the conspicuous abundance of dead-crowned northern rata on Kapiti Island, "especially on exposed spurs," and commented (p. 1): "That this should have been the case as early as 1907 is of particular interest at the present day when the death of rata–kamahi forest on a large scale in Westland and on a smaller scale in the Ruahine Range has become a major problem." In their analyses of southern rata mortality in Westland, Chavasse, Hoy (1958), and Tyndale-Biscoe mentioned the occurrence of "even-aged" and "dense-canopied" stands. That is, it is obvious that all the earlier authors who were concerned about the possible importance of possum browsing were aware of possible long-term trends affecting current patterns, and of the probable catastrophic origin and even-age structure of much of the montane rata and kamahi.

Stewart and Veblen (1982) developed a quantitative model to describe the regeneration patterns of rata and kamahi. Both species were found to regenerate sparsely beneath canopy gaps and within old stands, but abundantly on sites devastated by natural disturbances, so that the occurrence of numerous even-aged stands can be seen as reflecting the importance of catastrophes in their regeneration patterns.

However, on a regional scale, such an emphasis on dynamics leads to the unlikely conclusion that the forests so far invaded and occupied by dense possum populations

are predominantly old and already moribund, whereas those outside the present range of possums are young and vigorous.

Other difficulties inherent in Veblen and Stewart's hypothesis are best expressed by reference to their review (1982*a*). They make considerable use of the pioneer survey reports collated by Chavasse (1955, unpublished). Although Chavasse and his colleagues had recorded differences of opinion about the causes of mortality of rata and kamahi, the occurrence of abundant possum sign wherever mortality was conspicuous and the absence of possums elsewhere, led to the consensus that browsing by possums was an important cause. But Veblen and Stewart argued (pp. 390–391) that the "possum explanation" left several unanswered questions, which will be discussed below:

(1) Why do many relatively young rata and kamahi appear totally healthy and vigorous . . . in the midst of older dead or dying individuals . . . ?
(2) Why, as observed by the 1955 inspection team (Tyndale-Biscoe 1955 [*in* Chavasse 1955, unpublished]; Hoy 1958) are numerous dead rata found on steep slopes while adjacent ridge summit stands and gentle slopes generally show much less excessive mortality?
(3) Why are some rata–kamahi forests (such as in the Catlins area in south-eastern Southland) unaffected . . . ?
(4) Why in the Westland forests are many of the dead trees of species that are only lightly browsed (e.g., Hall's totara [*Podocarpus totara*] and mountain cedar [*Libocedrus bidwillii*]) . . . ?

(1) Healthy young rata and kamahi certainly are a conspicuous feature of Westland forests, but they are rarely, if ever, diffusely distributed "in the midst of older dead or dying individuals." Young trees occur in even-aged stands of up to several hectares in extent, typically on sites associated with landslides on hill faces or exposed to gales on upper slopes and ridges, i.e., sites affected by natural catastrophes.

These close-canopied stands are not favorable habitat for possums, as illustrated by the finding of fecal pellets on only 6% of 42 plots beneath a close-canopied hill face stand, when pellets occurred on 33% of 159 plots beneath more diffuse, multitiered stands close by (B. Warburton, personal communication). Veblen and Stewart (1982*a*:392) suggested that lower numbers may be the consequence of a lower diversity of palatable food plants within close-canopied stands. The availability of dry nest sites, dry traveling conditions, display sites on emergent trees, and other habitat attributes also undoubtedly influence the preferences of possums, and so influence their abundance. Whatever the balance of factors may be in any particular place, numbers of possums are low in young stands, as possum trappers, pest controllers, and biologists know or soon learn.

In addition, young trees appear to be more tolerant of browsing (Payton, this issue), since they exhibit more vigorous responses to the experimental removal of leaves than do old trees. Payton has suggested that, at least during the pre-peak stages of increase of possums, this is consistent with mortality of *Metrosideros umbellata* being confined to more mature trees.

(2) Veblen and Stewart's second question about mortality patterns on steep slopes and summit ridges does not convey the full substance of the writing of Hoy (1958) or Tyndale-Biscoe, to whom they attribute the observation. Those authors described healthy ridge-top stands as young and "close-canopied" or "even-aged," which are unfavorable to possums as already discussed. Tyndale-Biscoe noted cold, damp conditions and low possum numbers within a ridge-top stand where large rata appeared to be healthy. Both these examples are special cases. Coleman, Gillman, and Green (1980) showed that in the Haupiri area of Westland, ridges generally contain the highest proportion of rata and kamahi, the two principal food plants for possums. These authors and Bamford (1970) commented also on the concentration of possums in relatively dry, open sites, typically on the ridges and steep faces. Therefore, although possums may travel up to $3\frac{1}{2}$ km between shelter and food (Gilmore 1967), they typically feed on preferred species growing nearest to their shelter (Gilmore 1967, Jolly 1976), so that ridge stands and steep face stands are usually the earliest occupied and most heavily defoliated. Furthermore, groups of possums concentrate their feeding on individual trees (Meads 1976)

until these are more or less defoliated or dead, and then shift to their neighbors, in a dominoes-like succession, until the preferred species are depleted and the possum population declines.

Less excessive mortality on gentle slopes is also related to preferred habitat for possums. Gentler slopes usually are damper and contain higher proportions of relatively unpalatable species (such as *Quintinia acutifolia*, *Griselinia littoralis*, *Dacrydium cupressinum*, and *Podocarpus ferrugineus*). Less excessive mortality is therefore a consequence of fewer possums and a greater proportion of trees not vulnerable to their browsing. There is no evidence to suggest that the mortality rate among preferred species on such sites is less than it is elsewhere. Further, in forests on gentler terrain away from gullies, the seral scrub component is smaller because the land is less prone to slipping. Since *Fuchsia excorticata*, the typical dominant of the scrub, is an important summer food for possums (it is deciduous), forest areas that include a large component of seral scrub support higher densities of possums and sustain more severe browsing as a consequence. This relationship probably explains the abundance of surviving and profusely flowering rata on some forested valley floors (e.g., Waiho River, Westland), whereas upslope, browsing by possums and dieback are conspicuous and severe.

(3) The Catlins forests of southeastern South Island provide an intriguing contrast to those in the western mountains. Although rata and kamahi survive there in relatively good health despite a century of occupation by introduced mammals, it must be emphasized that they are not altogether "unaffected." Noticeable dieback of rata occurs in several places (R. Allen, personal communication), but the level of browsing is, by Westland standards, only moderate.

Moderation of the effect of browsing in eastern regions involves many species besides the forest dominants, and is characteristic of eastern regions throughout New Zealand. It therefore seems necessary to consider all the evidence that identifies them as a special case rather than as an unanswered question.

Greenwood and Atkinson (1977) catalogued the incidence of the divaricating growth habit, of thorns, astringent tastes, and other characteristics of shrubs and forbs, which they interpreted as adaptations to browsing by the extinct moas (Ratitae). Extending their argument, I think it is equally reasonable to interpret the deciduous habit in New Zealand dicotylous shrubs as an adaptation to browsing. Most, if not all, of the 19 species (e.g., *Fuchsia*, *Aristotelia*, *Muehlenbeckia*, *Discaria*, *Plagianthus*, *Carmichaelia*, *Hoheria*) are low-statured shrubs. They are now preferred foods of the introduced mammals (a red-colored form of *Fuchsia excorticata* common in many eastern places is an outstanding exception), and are typically found early in successions, on forest edges, and in open places of the drier eastern regions. [This interpretation differs from the more widely accepted view that the deciduous habit is an adaptation to low winter temperatures, e.g., see Dumbleton (1967).] Of the 35 indigenous species considered to be toxic (Connor 1977) or distasteful (Greenwood and Atkinson 1977), nearly all are also pioneer or early seral species (*Coriaria*, *Myoporum*, *Solanum*, *Urtica*, *Sophora*, *Hedycarya*, *Brachyglottis*, *Melicytus*, *Pteridium*). Only one apparently toxic tree (*Laurelia*) reaches the high forest canopy. These observations reinforce Greenwood and Atkinson's (1977) analysis, for it can scarcely be a coincidence that browse-tolerant or browse-resistant species (as defined above) are more common on forest edges, open country, river banks, swampy ground, and coastal dunes. Such sites are indicated by archaeological and subfossil remains to have been the main habitat of the moas. Thus, while the survival of rata in the east raises many questions, these center on a better understanding of evolutionary biology of the entire biome, not on an apparent contradiction of less severe browsing than in western districts.

(4) As with the Catlins forests, the conspicuous abundance of dead or dying mountain cedar and Hall's totara is only obscurely if at all related to the effects of possums. Coleman, Gillman, and Green (1980) noted that dead cedar seem to stand for decades,

giving an erroneous impression of mortality rates and causes. This is consistent with the fact that the timbers of cedar and Hall's totara are very durable (Cockayne and Turner 1938, Harris 1977). It is also reminiscent of the abundance of dead-crowned *Nothofagus fusca* (a very durable timber tree) in beech forests throughout New Zealand.

Veblen and Stewart (1982*b*) examined the dynamics of cedar in five localities on the western, northern, and eastern flanks of the southern Alps of South Island, and concluded that its population structure can be interpreted from its regeneration ecology. Cedar is relatively intolerant of shade, and its regeneration can be generalized into catastrophic and gap phase modes that are more or less correlated with the occurrence of storms and landslides. They also showed this for southern rata and kamahi (Stewart and Veblen 1982).

Nevertheless, several New Zealand ecologists have drawn attention to an apparent long-term regression of vigor, or imbalance in the structure of the slower-growing conifers. For example, Elder (1965:43) described *Libocedrus–Dacrydium* associations in the Ruahine Range of North Island as a "ghost of a formation" and down-slope migration, which in some areas is indicated by cedar logs on what is now alpine grassland (p. 45). He interpreted these patterns as evidence of a change extending over several generations, which in a species of at least a 500 yr life-span (Wardle 1978), implies a change over several centuries. Wardle (1978) summarized evidence of a "regeneration gap" during recent centuries, and also commented on the apparent senescence of many stands of cedar. In some montane areas, dead trees are conspicuous, regardless of the presence or absence of possums. In most eastern areas, where the conversion of forests to pastures has left only remnant stands or isolated trees in gullies and on higher ground, many trees have died back, possibly because of drought stress, possum browsing, or other causes.

It now also seems likely that both these species are generally browsed by possums. Hall's totara is variously recorded as lightly to heavily browsed (Coleman, Gillman, and Green 1980, Gilmore 1967, Kean and Pracy 1953, Mason 1958, Wardle 1978). Distinctive possum browsing has not been previously recorded on cedar, a whip-cord branchlet tree (Coleman, Gillman, and Green 1980), but Coleman (personal communication) recently found that cedar fragments comprised 8% of the leaf food in possum stomachs collected within the higher-altitude forests at Haupiri in Westland. Thus, on these slow-growing species, the significance of possum browsing may be greater than is implied by Veblen and Stewart (1982*b*).

Therefore, at least three possible (but not mutually exclusive) interpretations can be made of the conspicuous abundance of dead cedar and Hall's totara: It may reflect the durability of their timbers; it may be due to possums; it may reflect some long-term change. But of these, only Elder's (1965) observations on down-slope retreat of North Island cedar require explanations such as prehistoric cultural interference or long-term climate change. Those remaining are explicable in terms of modern land-use practices, possum browsing, and the autecology of the species. It therefore seems unnecessary to introduce this topic as an "unanswered question" in a consideration of the effects of possums in the Westland montane rata–kamahi.

The relevance of the dynamics of rata and kamahi as the basis of widespread dieback therefore stands as the only essential question. If dynamics are the critical element of the possum problem, as implied by Veblen and Stewart (1982*a*), then we must also suppose that the climatic and tectonic history of New Zealand during recent centuries has synchronized regeneration, growth, and senescence of the mixed hardwood forests to such a degree that synchronous dieback and collapse was bound to occur in the mid-twentieth century, or, as stated elsewhere: Collapse of the Ruahine forests was only a matter of time (Mosley 1978); the dramatic changes in the forests of the South Island are due to geologic and meteorologic events (Veblen and Stewart 1982*a*); natural

disturbances have a predominant influence on the dynamics of the forests of central Westland (Stewart and Veblen 1982).

I reject such conclusions, for the reasons stated throughout this review; the first-hand accounts of lethally heavy possum browsing, the repeated coincidence of increasing possum numbers and collapse or excessive mortality of preferred food species, the absence of notable dieback where possums do not occur, the recovery of trees protected from possums, and the experimental simulation of browsing by removing leaves. These facts all point the same way. Even the apparent immunity of young close-canopied stands of southern rata can be foreseen as a temporary respite, for if the past is a guide to the future, it can only be predicted that possums will lethally browse the trees as they approach maturity. Therefore, in view of the extensive collapse that has occurred in the past, and the scarcity of regeneration (particularly of rata) in damaged forests (Allen and Rose, this issue), I can see no justification for the view that "there is no basis for inferring a radical shift in forest type, even though fluctuations in the relevant abundance of the dominant tree species may be expected" (Stewart and Veblen 1982:70).

Both this topic and these conclusions are of considerable concern to forest managers because of their central importance to the question: What, if anything, should be done about possums in the forests? It is an unpalatable choice: Leave possums alone, or persevere with an expensive and apparently never-ending control program as the only practicable means by which the rata–kamahi forests and their associated scrublands can be maintained.

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